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INFLUENCE OF THE LEAF UPON ROOT FORMATION AND GEOTROPIC CURVATURE IN THE STEM OF *BRYOPHYLLUM CALYGINUM* AND THE POSSIBIL- ITY OF A HORMONE THEORY OF THESE PRO- CESSES

JACQUES LOEB

(WITH THIRTY FIGURES)

In two former publications¹ it was shown that while the stem of *Bryophyllum calycinum* prevents or retards the development of roots and shoots in the notches of a leaf, conversely the leaf accelerates the development of roots and shoots in a stem; since in a stem deprived of all leaves the roots and shoots develop later and grow more slowly than if a leaf is left on the stem. The two phenomena found a common explanation in the assumption that the leaf furnishes substances to the stem which accelerate the organ formation in the latter, while if these substances are not "sucked away" from the leaf by the stem they will accelerate the growth of roots and shoots in the notches of the leaf. These substances may be water or solutes.

In these experiments it was noticed that the leaf has also an accelerating effect upon the geotropic curvature of the stem. When stems of *Bryophyllum* are suspended horizontally by 2 threads in a jar saturated with water vapor, they will bend, becoming convex on the lower, and concave on the upper side (fig. 1), and this bending continues until finally the stems assume the shape of a U. This geotropic bending is a slow process when the stem contains no leaf, but is considerably accelerated if a leaf is left on the stem (fig. 1). The position of the leaf has a great influence, not only on the velocity of the geotropic bending and the region of the stem in which it occurs, but also upon the formation of organs in the stem. The description of this influence and of the apparently close connection between the two groups of phenomena will form the subject of this paper.

¹ LOEB, J., BOT. GAZ. 60:249-276. 1915; 62:293-302. 1916.

Straight stems, at least 10 cm. long, were selected for these experiments. The growing region and the 2 apical nodes were removed, the pieces chosen for experimentation containing about 4-7 or 8 nodes. Each stem was suspended horizontally by 2 threads (fig. 1), one at each end, in a jar the bottom of which was filled with water. The jar was loosely covered with a glass plate so that the stems were surrounded by an atmosphere almost completely saturated with water vapor.

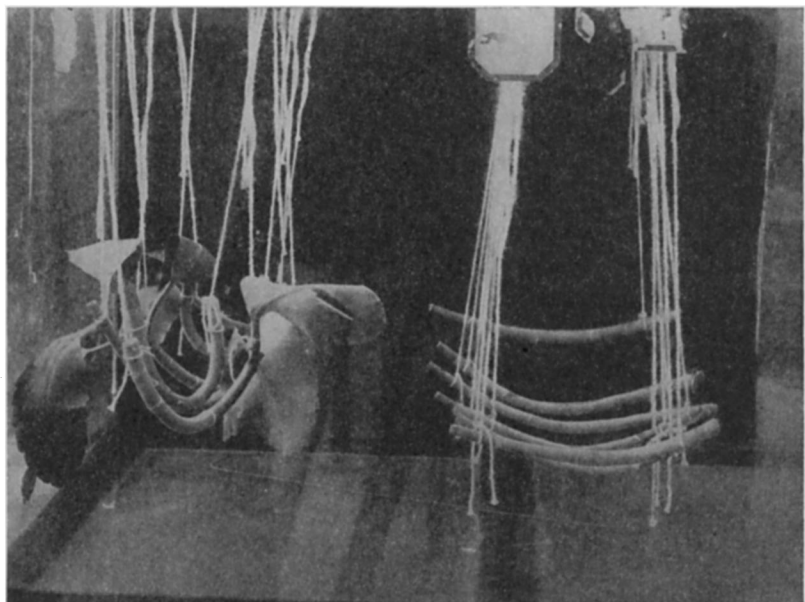


FIG. 1

The writer was rather surprised to find that stems deprived of their growing region should show geotropic curvatures. These curvatures were not confined to the nodes as is the case in grasses, but whole regions of the stem, both nodes and internodes, bent (fig. 1). We shall see later that the bending was accomplished by an increase in the length of the cortex of the under side of the horizontally placed stem, while the upper side of the stem was bent passively as a consequence of this growth.

I. INFLUENCE OF THE PRESENCE AND ABSENCE OF LEAVES

Fig. 1 illustrates the influence of the presence and absence of leaves upon the rapidity of geotropic curvature in the stems. The 6 stems to the right had no leaves and bent very slowly; the 6 stems to the left had each 2 leaves at the most apical node (while the other leaves were removed) and bent much more rapidly. The photograph was taken on the eleventh day after the experiment was begun. It is noticeable also that the stems containing leaves

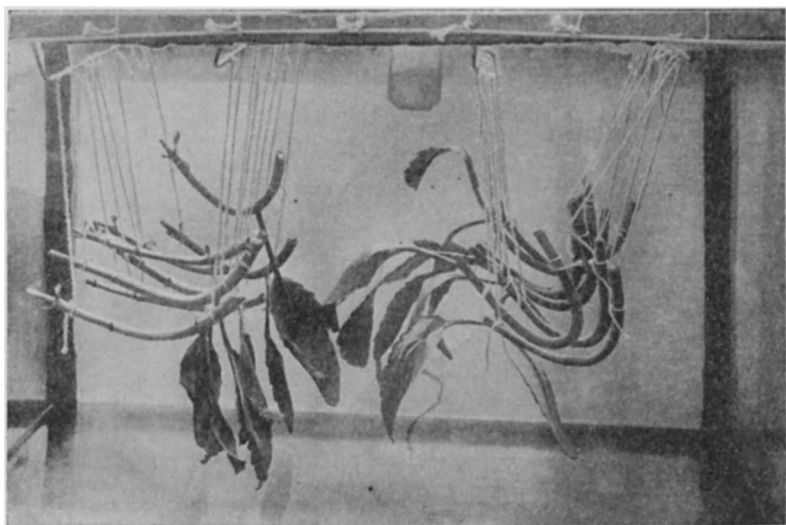


FIG. 2

formed roots (in their basal nodes) much more rapidly than the stems deprived of all leaves. This experiment, representing the accelerating influence of the apical leaves upon both root formation and geotropic curvature, never fails; and the same may be said of most of the experiments described in the following pages.

II. INFLUENCE OF THE POSITION OF THE LEAF ON THE STEM UPON GEOTROPIC CURVATURE AND ORGAN FORMATION

In the following experiment only one leaf was left on the stem. It was found that it made a great difference whether this leaf was at the apex or at the base. This is illustrated by fig. 2. On the

right hand in the photograph are 6 stems having one leaf left at the apex. These stems bent so rapidly and strongly that they soon reached a U-shape. On the left are 6 stems having a leaf left at the base. In this case the curvature is generally much less than

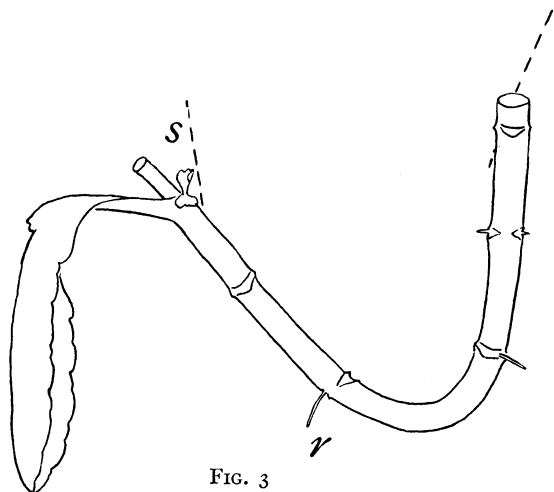


FIG. 3

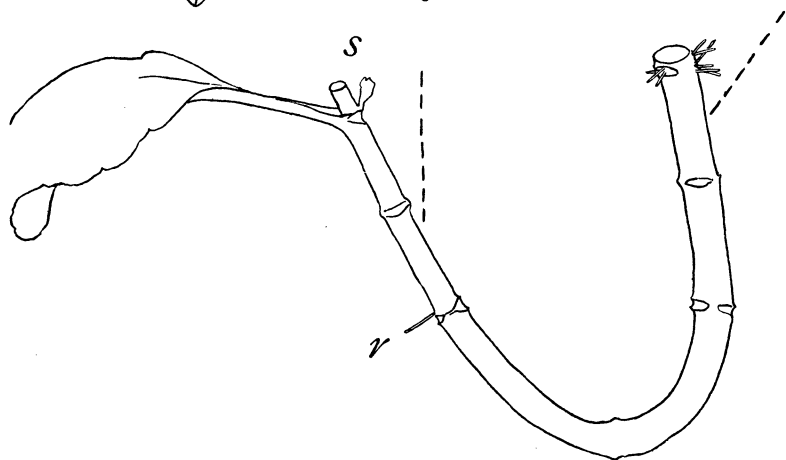


FIG. 4

when the leaf is at the apex. Both groups of stems had been suspended horizontally and both had been put into the jar at the same time. The photograph was taken on the eleventh day. This experiment also is always successful.

It is noticeable, incidentally, that while the leaf at the base accelerates the shoot formation, the one at the apex accelerates root formation. The more rapid geotropic curvature occurs in those stems in which the root formation is favored.

Aside from the influence of the position of the leaf upon the velocity and extent of the curvature, an equally striking influence exists between the position of the leaf and the localization of the curvature in the stem. When the leaf is at the apex, the curva-

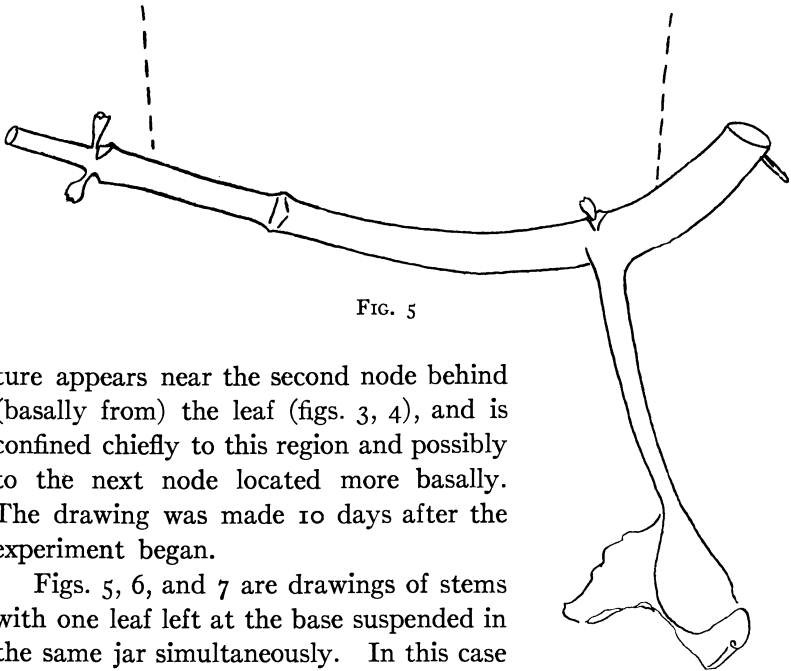


FIG. 5

ture appears near the second node behind (basally from) the leaf (figs. 3, 4), and is confined chiefly to this region and possibly to the next node located more basally. The drawing was made 10 days after the experiment began.

Figs. 5, 6, and 7 are drawings of stems with one leaf left at the base suspended in the same jar simultaneously. In this case little curvature takes place and the curvature which occurs is near the region where the leaf is located. Fig. 6 is an extreme case. It seems that the amount of curvature increases with the length of the piece of internode left behind the basal leaf. The photograph in fig. 2 shows also the difference in the localization of curvature according to whether the leaf left is at the apex or at the base.

In the experiments thus far mentioned the leaf was on the lower side of the stem. When the leaf is left on the upper side of a

horizontally suspended stem, the geotropic bending is slower than when it is on the lower side, but the bending will also be much more rapid and more intense when the leaf is left at the apex (figs. 8, 9, 10) than when it is left at the base (figs. 11, 12, 13). In the latter case the bending is again slight, and what little curvature occurs is confined to the immediate neighborhood of the basal leaf. Fig. 13

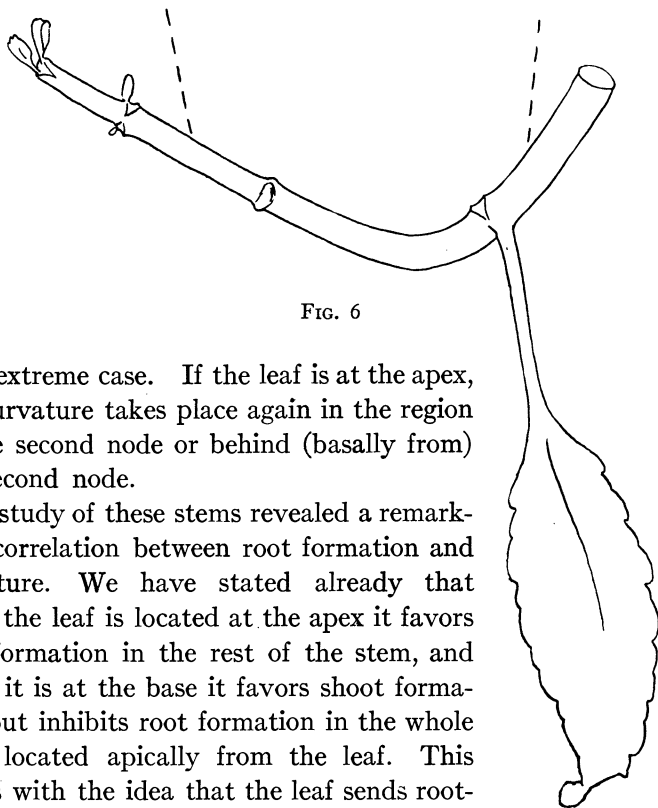
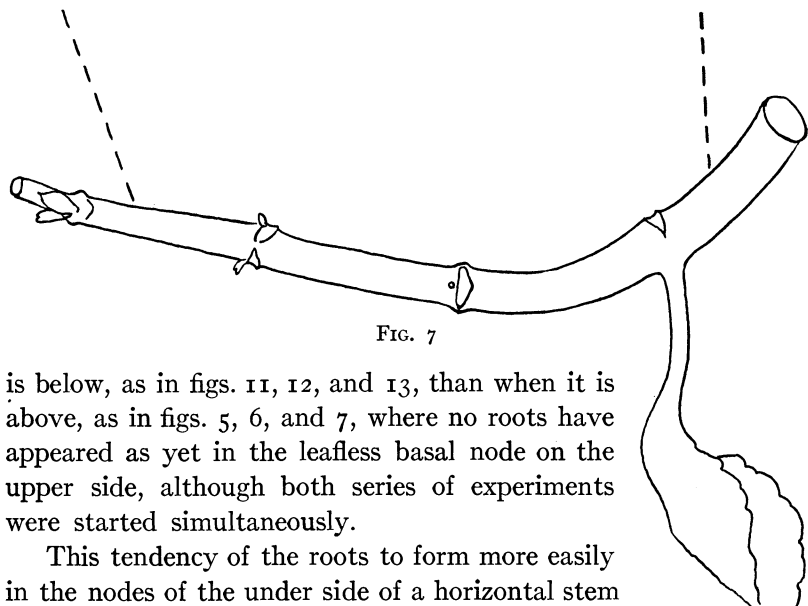


FIG. 6

is an extreme case. If the leaf is at the apex, the curvature takes place again in the region of the second node or behind (basally from) the second node.

A study of these stems revealed a remarkable correlation between root formation and curvature. We have stated already that when the leaf is located at the apex it favors root formation in the rest of the stem, and when it is at the base it favors shoot formation but inhibits root formation in the whole stem located apically from the leaf. This agrees with the idea that the leaf sends root-forming substances toward the base and shoot-forming substances toward the apex. We notice that the geotropic curvature is favored or accelerated most in those stems in which an apically located leaf is left, and in such stems root formation is favored also. The correlation between root formation and geotropic curvature is still more striking, however, if we consider the location of the roots formed. When the leaf left is at the apex,

roots usually appear in the second (and often the fourth) node behind the leaf, where the geotropic curvature also begins. This is obvious in *r*, figs. 3, 4, 8, 9, and 10. When the leaf left is at the base, the root formation is considerably less (as is also the geotropic curvature), and what there is of root formation occurs again in the region where the main geotropic curvature also occurs; namely, in the lower basal node (*r*, figs. 11, 12, 13). When the leaf is at the base, root formation is more favored when the leafless basal node



is below, as in figs. 11, 12, and 13, than when it is above, as in figs. 5, 6, and 7, where no roots have appeared as yet in the leafless basal node on the upper side, although both series of experiments were started simultaneously.

This tendency of the roots to form more easily in the nodes of the under side of a horizontal stem is an important link in the chain of circumstances connecting root formation and geotropic curvature, since the growth causing this curvature is confined to the cortex of the under side of the stem.

III. EXPERIMENTS ON STEMS SPLIT LONGITUDINALLY

In order to find out the mechanism of geotropic curvature, stems were split lengthwise and suspended horizontally in jars saturated with water vapor. Each half stem had one leaf left either at the apex or at the base. Figs. 14-20 give the typical results of a series of such experiments on the seventeenth day.

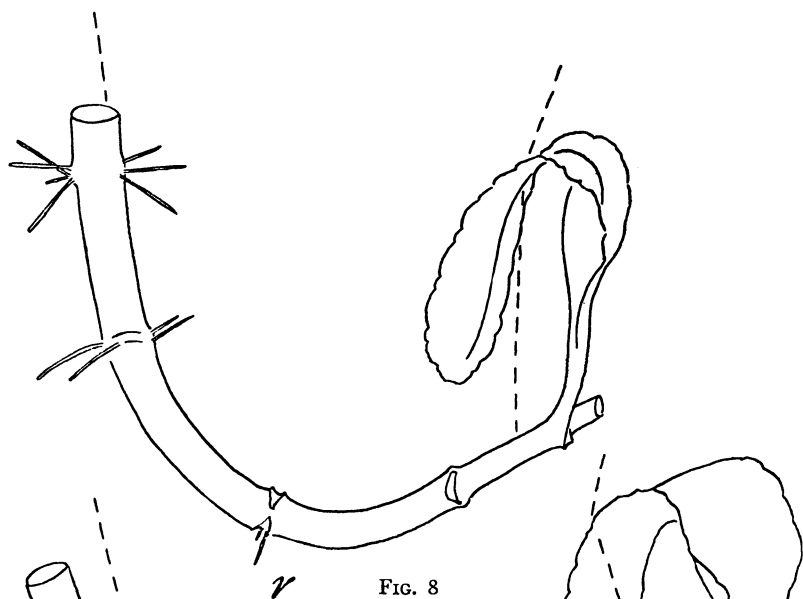


FIG. 8

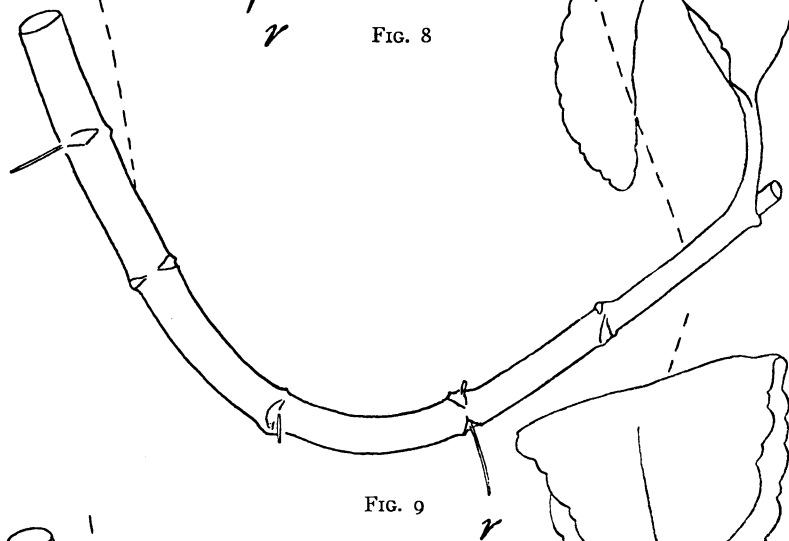


FIG. 9

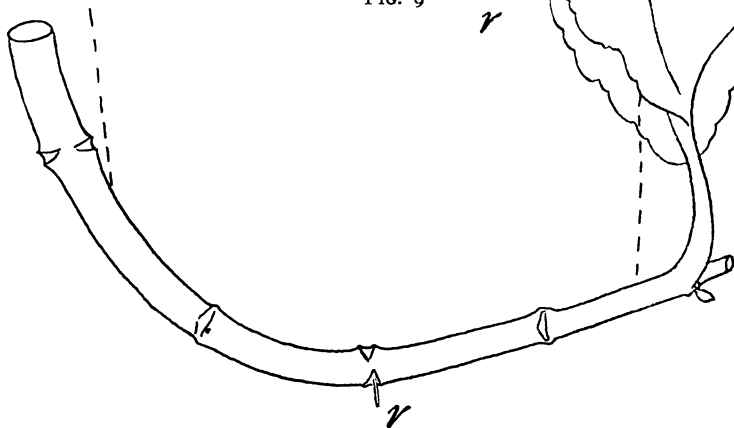


FIG. 10

Figs. 14, 15, 16, and 17 give the appearance of the lower halves of the stems (that is, stems suspended horizontally in such a way that

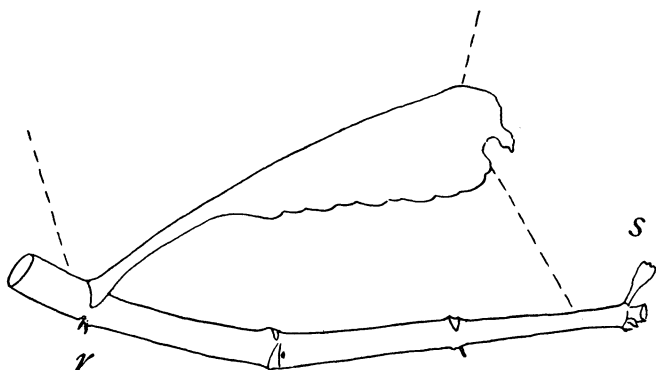


FIG. 11

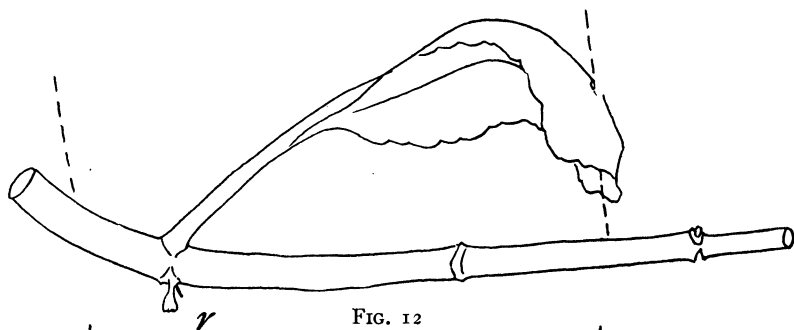


FIG. 12

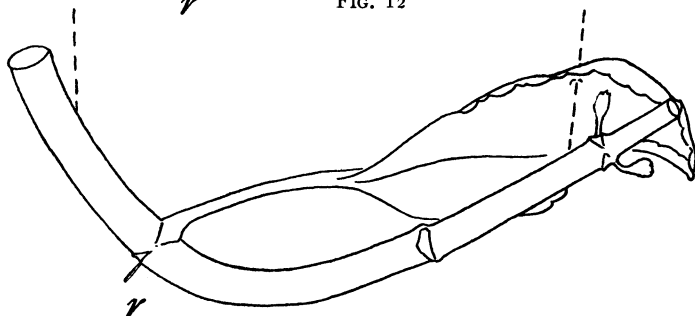


FIG. 13

the cortex was below, and the cut surface above) on the seventeenth day. When the apical leaf is preserved, the bending is rapid and extensive, as in fig. 17. When the basal leaf is preserved (figs. 15,

16), either no bending occurs, as in fig. 15, or it is confined to the region of the leaf or of the first node in front of the basal leaf (fig. 16). When no leaf is left, as in fig. 14, a slow bending takes

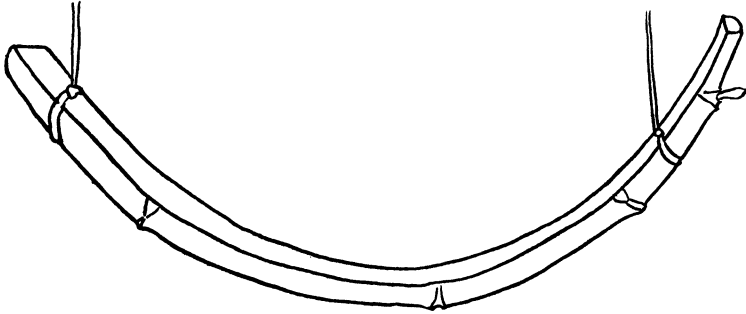


FIG. 14

place, more rapid and extensive than in fig. 15, but less rapid than when the apical leaf is left, as in fig. 17. In the other halves of the stem which were suspended with the cortex above (figs. 18, 19, 20), practically no geotropic bending takes place, for the reason that

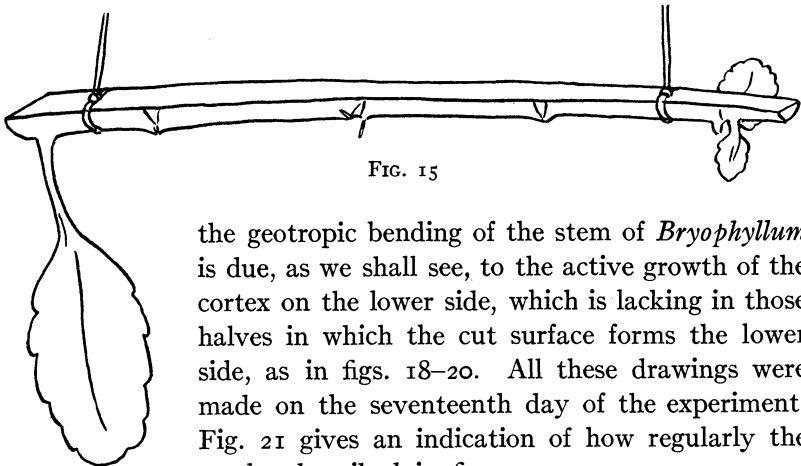


FIG. 15

the geotropic bending of the stem of *Bryophyllum* is due, as we shall see, to the active growth of the cortex on the lower side, which is lacking in those halves in which the cut surface forms the lower side, as in figs. 18-20. All these drawings were made on the seventeenth day of the experiment. Fig. 21 gives an indication of how regularly the results described in figs. 14-17 occur.

It was of interest to study the reaction of split stems in which the leaf was above and the cortex below. For this purpose it was necessary to split the stem only to the apical or basal node in which the leaf was preserved (figs. 22, 23), but not in its entire length.

When the leaf is at the apex and above (fig. 22), geotropic curvature of the stem occurs, but not so rapidly as when the leaf is below;

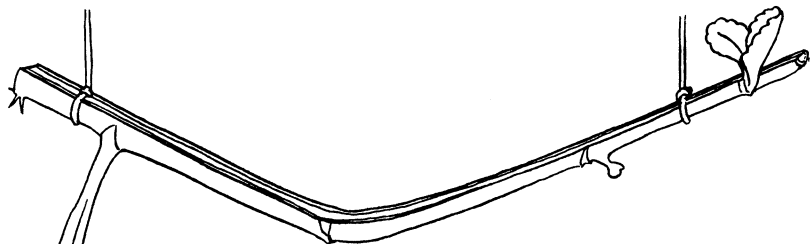


FIG. 16

the location of the curvature is again in the region of and basally from the second node behind (basally from) the leaf. When the leaf is at the base and above (fig. 23), no curvature ensues, at least for a long time. The drawings were made on the seventeenth day.

The correlation between root formation and geotropic curvature is again striking. When in a longitudinally split stem the apical leaf is preserved and the cortex below, as in figs. 18 and 22, root formation occurs in the second node behind the leaf, in the region

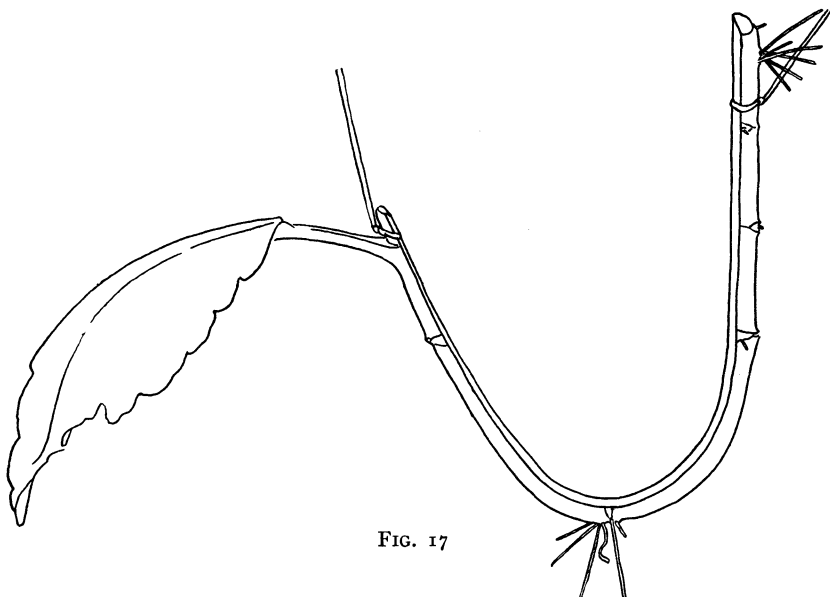


FIG. 17

where the curvature also occurs. Roots appear also at the basal nodes and sometimes at the cut basal surface of these

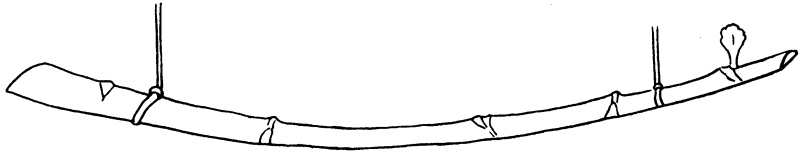


FIG. 18

stems. When the basal leaf is preserved and this leaf is below (fig. 15), no root formation takes place generally, or not for a long

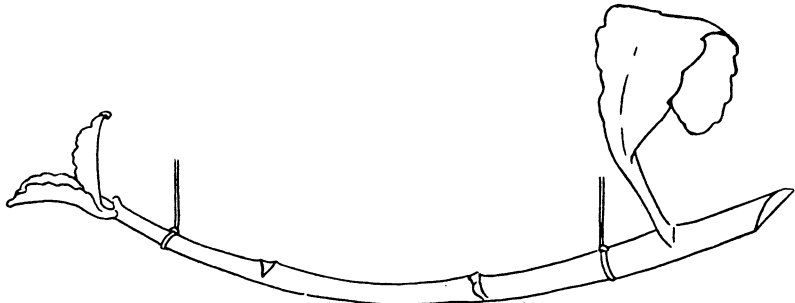


FIG. 19

time at least; while when the leaf is above (fig. 23), such root formation takes place in the basal node on the under side of the stem opposite the leaf. When the cortex is above and the leaf at the apex, root formation will occur, but chiefly or most rapidly in the basal node, and later in the next or the 2 nodes next to them (fig. 20). When the leaf is at the base or when the stem has no leaf, no root formation occurs in the cases where the cortex is above, at least for a long time.

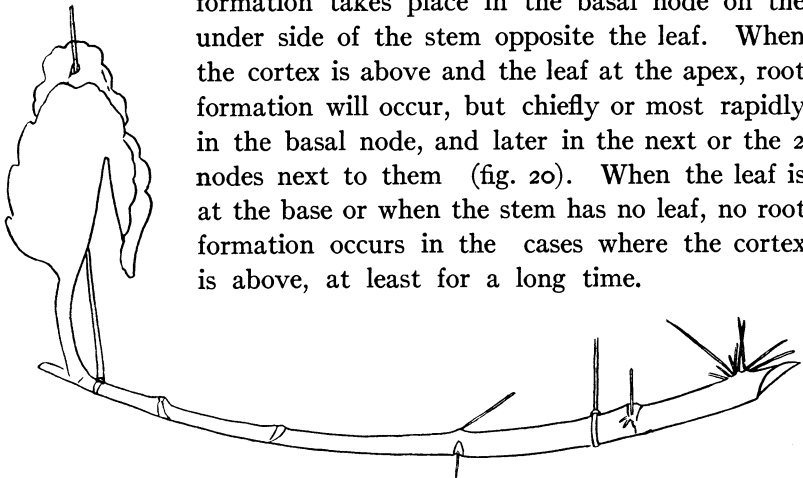


FIG. 20

IV. MECHANISM OF GEOTROPIC CURVATURE IN *BRYOPHYLLUM* CALYCINUM

These experiments with split stems were used to obtain a more definite idea concerning the mechanism of the geotropic bending.

Immediately after the stems were split, marks were made with India ink on the cortex at a distance of 1 cm. from each other and then the stems were suspended horizontally, one-half of the split stems having their cortex below, the others having their cortex

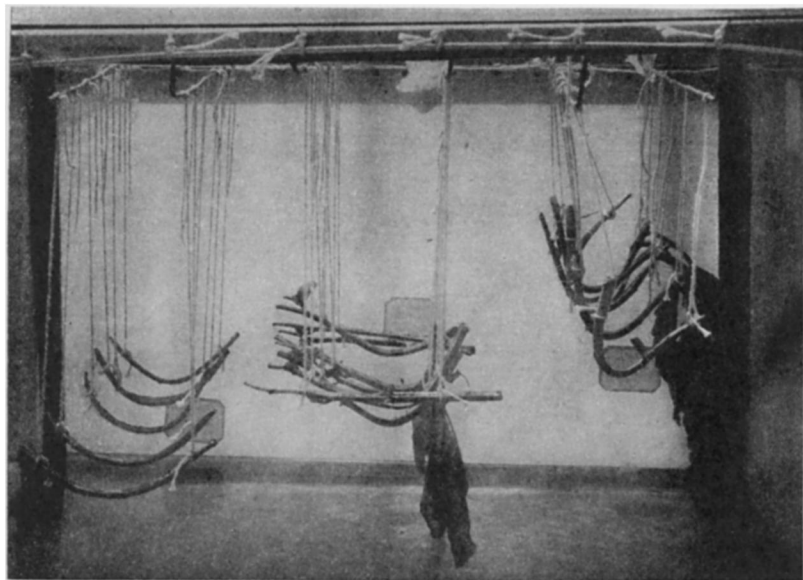


FIG. 21

above. Stems with an apical leaf were used for the purpose (like those in figs. 17, 20). After 10 days, when the halves with the cortex below had bent strongly, the displacement of the marks was ascertained. It was found that the marks on the halves in which the cortex was above and which had not bent were practically unchanged. The same was true of the marks in the non-bent regions of the other halves, where the cortex was below; while a growth of 15-20 per cent of the original length had taken place in the bent convex region of those stems having their cortex below.

Stems split lengthwise and with a leaf left at the most apical node were put horizontally into a jar saturated with water vapor. One-half of the stems were put with the cortex above (fig. 20), and one-half with the cortex below (fig. 17). Only the latter bent geotropically, the others showing only a slight concavity on the upper side, which may have been partly of a geotropic character, but which more likely was for the greater part, if not entirely, due

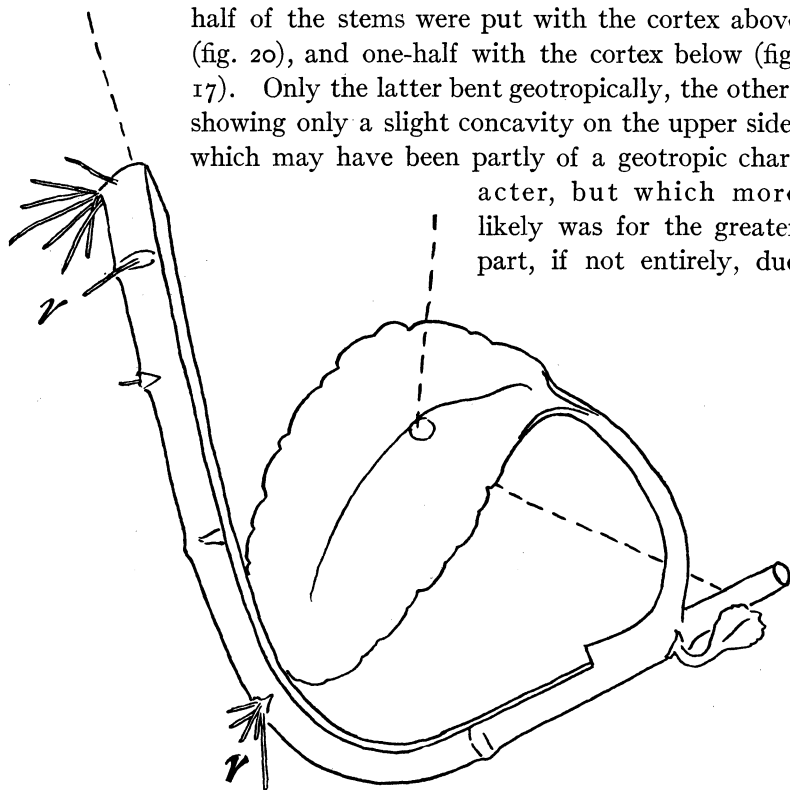


FIG. 22

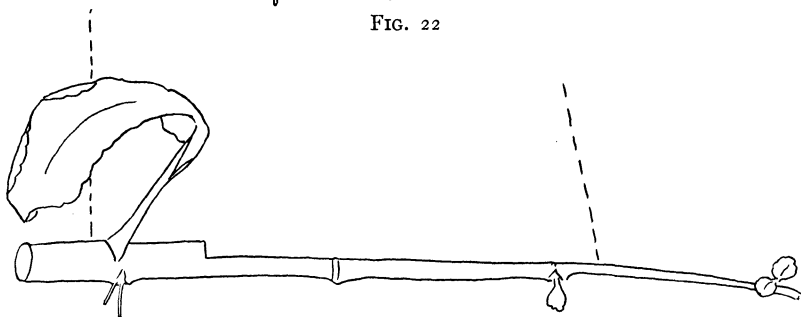


FIG. 23

to the tension of the cortex, which has a tendency to shorten in the longitudinal direction.

The experiment was begun June 21 and the measurements were taken on July 1. The original length of each piece of stem before the experiment was known from the India ink marks, the *final* length could be ascertained by direct measurement. First it was found that the length of the split stems which had been suspended with their cortex above was not altered, as shown in table I.

TABLE I
LENGTH OF SPLIT STEMS PLACED HORIZON-
TALLY WITH CORTEX ABOVE (IN CM.)

| At beginning of experi- ment (June 20) | At end of experiment (July 1) |
|---|----------------------------------|
| 9.0 | 9.0 |
| 11.0 | 10.8 |
| 10.0 | 10.0 |
| 14.0 | 13.8 |

Obviously no growth had taken place in these halves; there may possibly have been a slight shortening, but if this was the case it was so small that it was within the limits of error of measurement.

An altogether different condition was found in the other halves of the stems which had been suspended horizontally with their cortex below. Here an increase in length was found in the bent part of the stem, while the apical and basal ends which had not bent were practically unaltered also in regard to length. We designate the apical unbent region *A*, the central bent region of the stem *B*, and the unbent basal region *C*. The measurements of 4 stems are given in table II (p. 40).

It is obvious that an increase in length of 15-20 per cent took place in 10 days in the bent central region of the stem (basally from or around the second node behind the apical leaf), while the unbent basal and apical regions showed no distinct alteration of length.

Fig. 24 is a photograph of marked *whole* stems 9 days after the beginning of the experiment. The stems had been suspended horizontally in the jar; all had one apical leaf left. That part of the cortex which was below had stretched, while the cortex above was shortened. The India ink marks were 1 cm. distant and were made at the beginning of the experiment. The photograph shows the change in the position of the marks on the convex and concave sides in the bent region of the stem.

It is highly probable, if not certain, that the increase in length on the lower side of the horizontally placed stem takes place primarily in the cortex of the bending region and not in the pith or wood. This follows from the behavior of these 2 parts when the cortex of a bent (split or whole) stem is removed, and the rigidity of the cortex is compared with that of the pith and wood taken out.

TABLE II

| REGION OF STEM MEASURED | STEM I | | STEM II | | STEM III | | STEM IV | |
|----------------------------------|---------------------------|--------------------|---------------------------|--------------------|---------------------------|--------------------|---------------------------|--------------------|
| | Begin-ning of experi-ment | End of experi-ment | Begin-ning of experi-ment | End of experi-ment | Begin-ning of experi-ment | End of experi-ment | Begin-ning of experi-ment | End of experi-ment |
| A: non-bent apical part. | 3.0 cm. | 3.2 cm. | 3.0 cm. | 3.0 cm. | 4.0 cm. | 4.0 cm. | 4.0 cm. | 4.1 cm. |
| B: bent central part. | 4.0 | 4.9 | 5.0 | 5.7 | 6.0 | 7.0 | 4.0 | 4.85 |
| C: non-bent basal part. . . . | 2.0 | 2.0 | 3.0 | 3.0 | 5.0 | 5.0 | 4.0 | 4.15 |

If we remove the cortex on the lower (convex) side of a split geotropically bent stem, like that in fig. 17, we find that the rigidity of the cortex in the bent region is much greater than that of the wood or pith; the latter appears soft in comparison with the cortex of the bent region on the convex side of a geotropically bent stem. It is possible also that the increase in the rigidity of the cortex in this region may be due to a thickening of the cortex, a point which needs further investigation. Whatever the cause of this increase in rigidity may be, we reach the following conclusion regarding the mechanism of the geotropic bending of a horizontally suspended stem of *Bryophyllum calycinum*.

On the lower side of such a stem in a region the location of which depends upon the presence or absence, and, in the former case, upon the location of the leaf in the stem, the cortex begins to grow in length (and possibly in thickness). The wood, pith, and cortex on the upper side undergo no such growth. This increase in length (in one region) of the cortex on the lower side leads to a bending of the stem in which the lower side of a horizontally suspended stem becomes convex, the upper side concave.

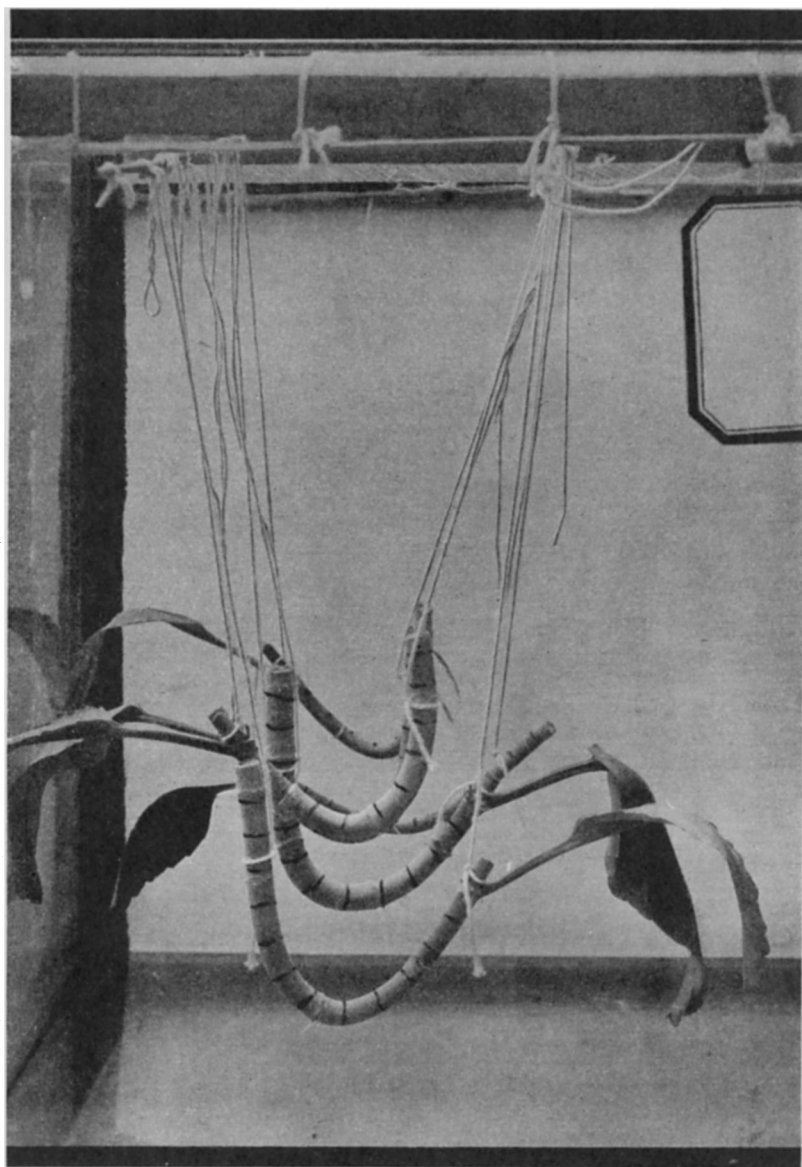


FIG. 24

Our investigation shows that this growing region of the cortex coincides with the region where early roots are formed. This suggests the possibility *that the geotropic growth of the cortex on the lower side of a horizontally suspended stem is due to a cause which is either closely associated or identical with the cause of root formation.*

If we assume with SACHS that there are specific root-forming substances, then the question presents itself whether we are not forced also to ascribe the geotropic curvature to the existence of specific geotropic substances or hormones; both substances having the tendency to collect on the lower side of a horizontally suspended stem; and both substances stimulating growth, the one of roots, the other of the cortex. On the basis of such an assumption we might understand why no or only an insignificant geotropic curvature takes place in a split stem when the cortex is on the upper side, the reason being that the geotropic substances settling at the lower side find no cortex which can grow and cause geotropic bending. This assumption will of course be a mere hypothesis until the existence of such hormones can be demonstrated directly.

V. FURTHER EXPERIMENTS ON THE INFLUENCE OF THE POSITION OF THE LEAF UPON THE GEOTROPIC BENDING OF A STEM

When we remove the cortex on the upper or lower side of a horizontally suspended stem of *Bryophyllum calycinum* (without removing the wood and pith), an extensive bending of the stem takes place instantly (fig. 25), the side on which the cortex is removed becoming convex. The mechanism of this phenomenon becomes clear on the assumption that the cortex is under a tension longitudinally which shortens the wood and pith. If this tension is removed on one side of the stem, the wood and pith on that side can stretch, while the wood and pith on the opposite side are held in check by the cortex. This leads to a considerable curvature whereby the side on which the cortex is preserved becomes concave (fig. 25). This curvature due to cortex tension is much stronger than the curvature which takes place instantly when we split a stem longitudinally. In this case not only the cortex but also the wood and pith are removed on one side of the stem, and hence the tendency of this side to stretch is considerably less than if only the cor-

tex is removed on one side. In the former case the stretching force of wood and pith on the side where the cortex is removed is lacking. Such stems show in a striking way the influence of the position of the leaf upon the geotropic curvature.

More than a dozen stems whose cortex was removed on the upper side were suspended horizontally (figs. 26, 27). Each stem had one leaf left, one-half of the stems having the leaf at the base (fig. 26), the other half having it at the apex (fig. 27). Only the latter bent geotropically, while the stems with the leaf at the basal end, not being able to overcome the resistance of the upper side of the pith and wood, did not undergo any geotropic bending. This shows that the geotropic growth of the cortex must be considerably less when the leaf is at the base than when it is at the apex.

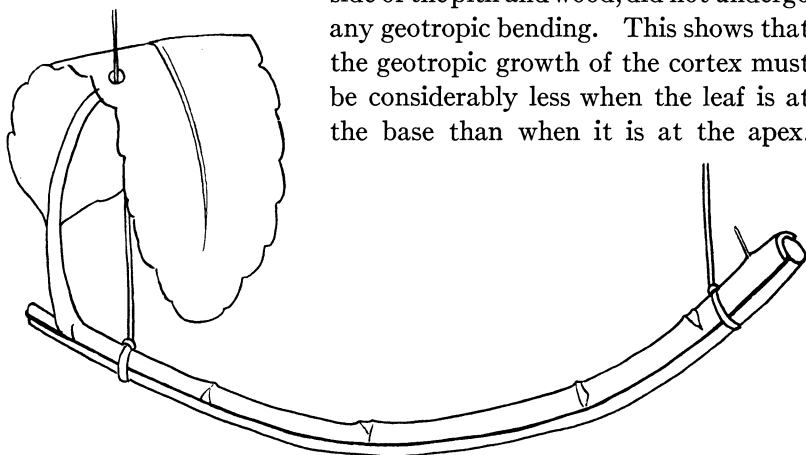


FIG. 25

When the cortex was above (fig. 25) and the leaf at the apex (or at the base), no or very little geotropic curvature ensued beyond the curvature due to the effect of the removal of the cortex on one side of the stem, which takes place instantly after the operation.

When the leaf is left at the apical end and the cortex below, as in fig. 27, the curvature occurs again in the region of the second node behind (basally from) the leaf; and in that node on the lower side the first roots develop (fig. 27). These drawings were made 9 days after the beginning of the experiment. If all the leaves are removed on such a stem it is no longer able to bend geotropically.

VI. FURTHER VARIATION OF THESE EXPERIMENTS

It is well known that the so-called geotropic "stimulus" goes around a corner, that is, around an incision. If we assume that the so-called "stimulus" is the flow of a liquid, we need not be surprised that it is able to go around a corner or around an incision in a stem. In a former paper (see footnote 1) we have shown that the "inhibition" of the stem upon the growth of the notches of a

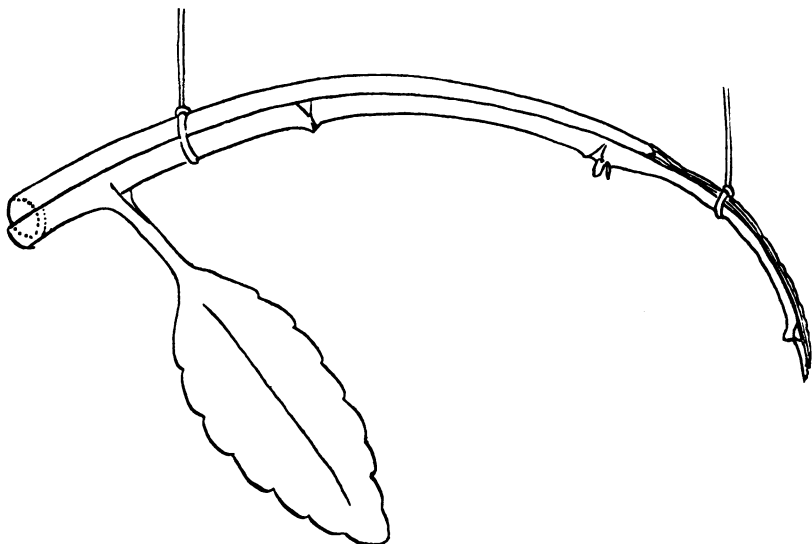


FIG. 26

leaf also goes around a corner in a leaf when incisions are made into such a leaf; and the mysterious character of the phenomenon disappeared with the recognition of the fact that the "inhibition" is the flow of certain substances (water or solutes) from the leaf into the stem through a system of interlinked channels which allows a flow in a zigzag around incisions. The same conception will explain in our opinion why a geotropic "stimulus" will flow around an incision in a stem, the "stimulus" like the "inhibition" being the flow of certain substances through the leaf or stem respectively.

Incisions were made into each internode of stems of *Bryophyllum calycinum*, at *a*, *b*, *c*, and *d* in figs. 28 and 29. The stems were suspended horizontally in a jar saturated with water vapor. Six

stems had one leaf at the apex and below (fig. 28), the other 6 had 2 leaves at the basal node (fig. 29). All of the stems with the leaf at the apex bent geotropically (though not as rapidly as stems without incisions), while those with the leaves at the base remained unbent. Figs. 28 and 29 show the difference after 10 days. In

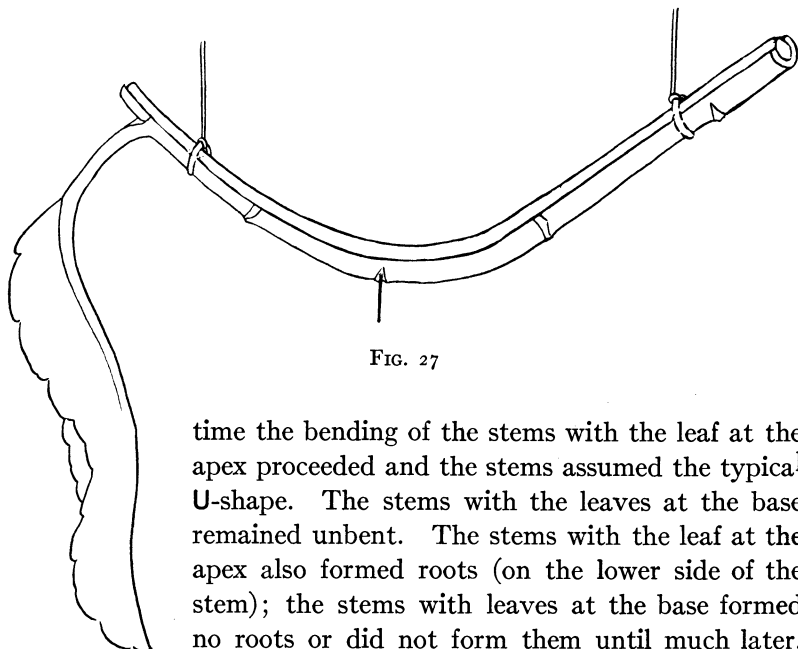


FIG. 27

time the bending of the stems with the leaf at the apex proceeded and the stems assumed the typical U-shape. The stems with the leaves at the base remained unbent. The stems with the leaf at the apex also formed roots (on the lower side of the stem); the stems with leaves at the base formed no roots or did not form them until much later.

VII. FORMATION OF ROOTS IN PASSIVELY BENT STEMS

We have seen that in stems suspended horizontally the roots have a tendency to form on the under side in the same region where the bending occurs. They form also at the basal nodes, both the upper and lower, but this fact does not concern us in this connection. The tendency of the roots to form on the lower side in that region which becomes convex might suggest the possibility that the root formation occurs in the convex region, not because it is the lower side, but because the convexity in itself might in some way favor root formation. The following experiment shows that the roots form on the lower side of a stem regardless of whether this lower side is concave or convex.

Stems were bent passively and fixed in this bent position by tying their ends to a piece of wood (fig. 30). Such pieces were then suspended in a jar saturated with water vapor. The experiments were made a year ago, before the writer was aware of the influence of the position of the leaf upon geotropic curvature and root formation, and in the expectation that passive bending of a stem would lead to the production of roots on the convex side of the stem. This was found not to be the case. Fig. 30 shows that numerous

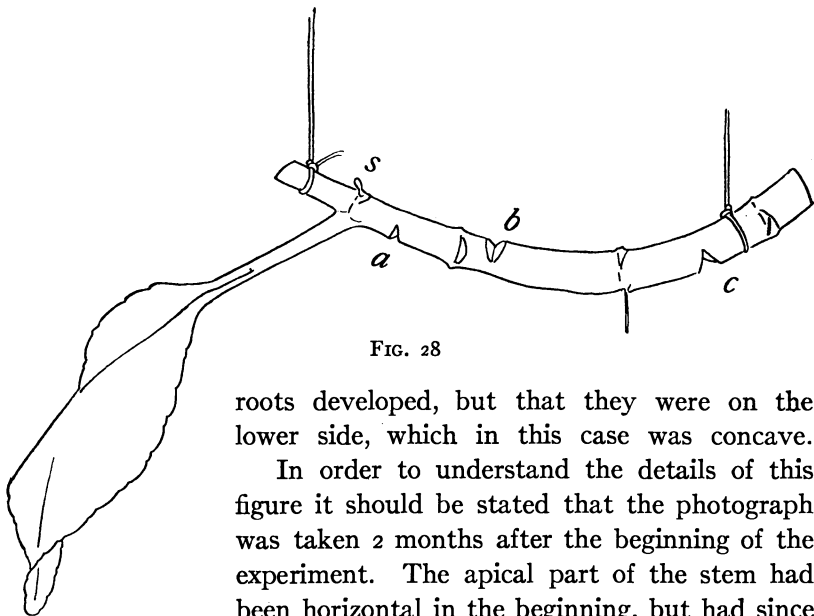


FIG. 28

roots developed, but that they were on the lower side, which in this case was concave.

In order to understand the details of this figure it should be stated that the photograph was taken 2 months after the beginning of the experiment. The apical part of the stem had been horizontal in the beginning, but had since bent upward, the bending taking place behind the second node. The side on which the roots were formed, therefore, had originally been the under side. The roots formed all along the lower side of that part of the stem which at first was in a horizontal position. Besides the small apical leaves, a large older leaf had been left on the stem, and from this leaf the stem was suspended. At the base of this large leaf and of the next 2 nodes a strong root formation took place. This is what we should expect on stems in which a leaf is left on the upper side.

Fig. 30 also illustrates in another way the influence of gravitation on root formation. The reader will notice that in the

horizontal region of the stem (basally from the large leaf from which the specimen was suspended) 2 large roots grew out from the internode. This occurs only after a long time and only on the lower side of a stem.

The experiment demonstrates, therefore, that roots will form on the concave side of a passively bent stem of *Bryophyllum calycinum* if this side is the under side of such a stem.

VIII. THEORETICAL REMARKS AND SUMMARY

1. The theoretical remarks may be brief. We believe that these experiments show first that in *Bryophyllum calycinum* the sub-

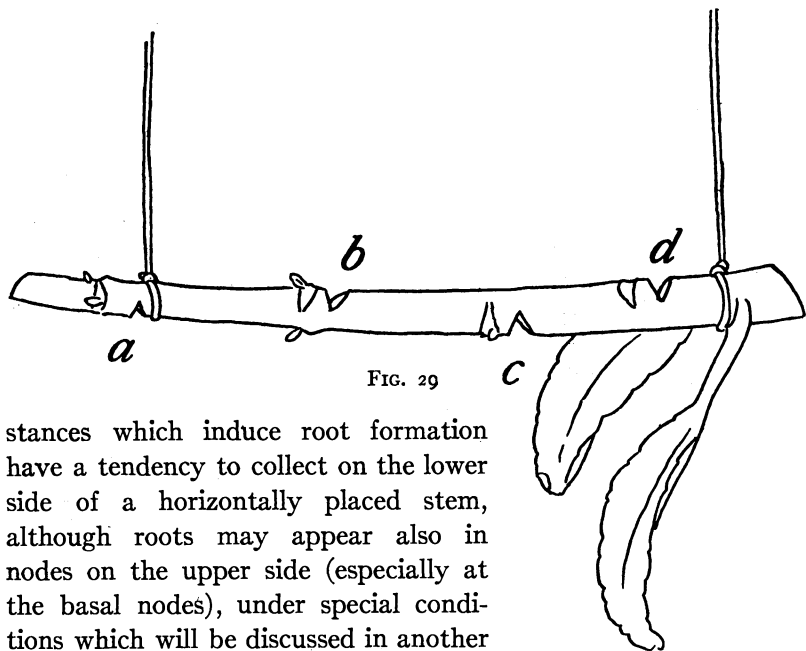


FIG. 29

stances which induce root formation have a tendency to collect on the lower side of a horizontally placed stem, although roots may appear also in nodes on the upper side (especially at the basal nodes), under special conditions which will be discussed in another paper. It is shown in this paper that a horizontally suspended stem of *Bryophyllum* will become concave on the upper side, and that this curvature, which will give such a piece a U-shape, is due to a longitudinal growth of the cortex on the under side of the horizontally suspended stem.

2. We have seen that a leafless stem bends much more slowly than a stem in which one or more leaves are preserved; and we find

also that the roots form more slowly in a leafless stem than in a stem with leaves. We find also that in a general way the

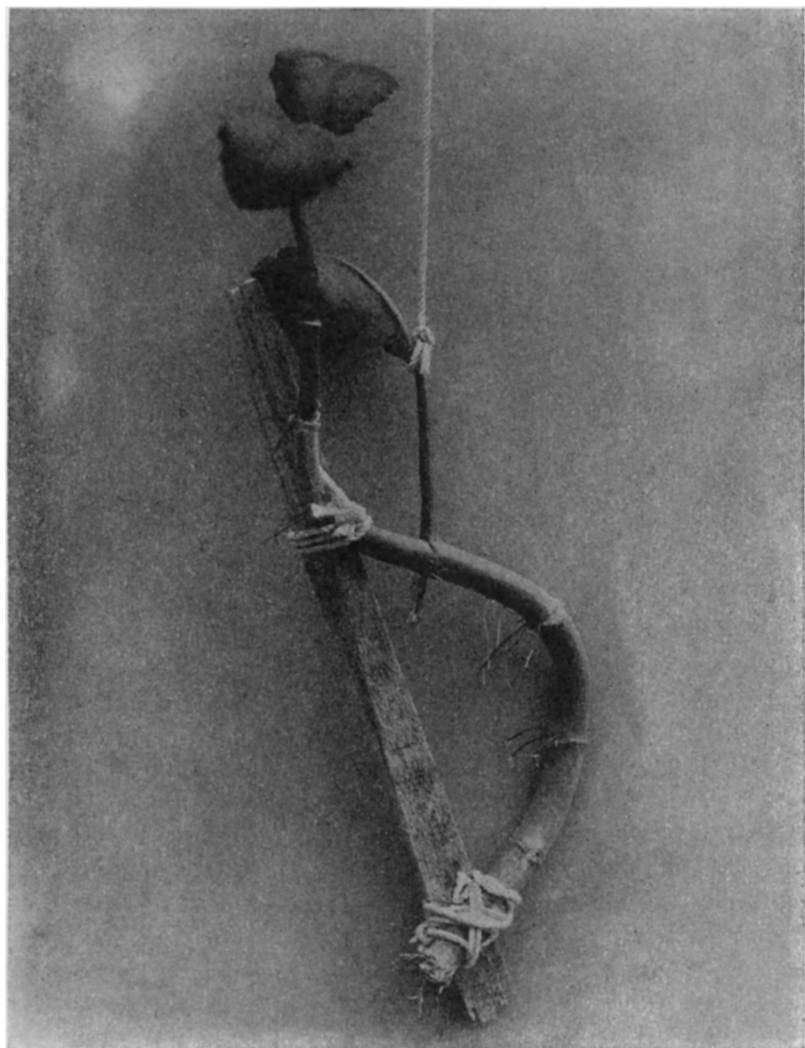


FIG. 30

amount of curvature and the amount of root formation vary in the same sense.

3. Both phenomena of geotropic curvature as well as of root formation depend in a striking way upon the position of the leaf on the stem. If in a horizontally suspended stem of *Bryophyllum* (in which the growing point is cut off) one leaf is preserved at the apex, and on the lower side of the stem, a rapid and very extensive geotropic curvature of the stem will take place, which is localized in the region basally from or around the second node from the leaf. The curvature is so extensive that the stem will assume the shape of a U with the concave side above. In such stems an extensive and rapid root formation will take place first in the second and fourth nodes behind the leaf on the lower side and also in the most basal nodes. The second and fourth nodes behind the leaf are therefore the centers of both kinds of growth in such a stem, namely, of the cortical growth which leads to the geotropic curvature and of the growth of roots. It should be pointed out also that in *Byrophyllum* the axes of successive nodes are always at right angles to each other, so that the favored nodes, the second and fourth behind the most apical one, all have the same orientation. It is quite possible that this structural peculiarity accounts for the fact that both root formation and geotropic curvature center around the second and fourth nodes behind a leaf left in the apex of an otherwise leafless stem.

4. If in a horizontally suspended stem only one leaf is left at the base of the stem (and on the lower side) the curvature is usually considerably less than in a stem with a leaf in the apex. The curvature in a stem with a basal leaf is confined to the region behind or around the leaf. It harmonizes with our previous statements that in such stems little or no root formation takes place, and that the root formation which occurs is confined to the node opposite the basal leaf and to the basal cut surface. When the piece of internode left behind the basal leaf is long, a more extensive curvature may occur than when the piece of internode left is short.

5. This difference in the influence of the apical and basal leaf can be made more striking when either the flow of substances in the stem is retarded (for example, by incisions in the stem) or when the resistance to the bending is made greater (by removing the cortex on the upper side of a horizontally placed stem whereby the

latter becomes concave on the lower side). In such cases geotropic curvature becomes possible only in stems with a leaf at the apex, but not in stems with a leaf at the base.

6. All these experiments become intelligible on the assumption that each leaf has a tendency to send shoot-forming substances toward the apex and root-forming substances toward the base of the stem. If it could be proved that in *Bryophyllum calycinum* a specific substance (hormone) is responsible for the geotropic growth (in the cortex of the lower side of a horizontally suspended stem), we might say that both substances show a tendency to collect on the lower side of a horizontally placed stem, and that the flow of both is influenced in the same way by the leaf. The apical leaf sends both substances toward the base of a stem, while the basal leaf acts as if it had a suction effect upon geotropic substances contained in the apical region. Such an idea suggests itself from the fact that a leafless stem has the center of its geotropic curvature in the middle (fig. 15), while a stem with a leaf at the base has either no curvature (fig. 16) or has it only in the region of the leaf.

While in *Bryophyllum* the hypothetical geotropic hormone is associated (or identical) with the root-forming hormone, in other plants the hypothetical geotropic substance might be associated with the shoot-forming hormone. This would explain the fact that in certain fir trees a horizontal branch next to the apex may suddenly become negatively geotropic when the apex is cut off. After the decapitation the (hypothetical) geotropic substance which before was flowing to the apex now can flow into the horizontal branches next to the apex, and the one which by chance gets a little more of the substance than the others will be the first to become vertical. After this the mechanical advantage due to the vertical position will favor the continued flow of these substances in this branch, which thus becomes the new apex.